REVIEW

Altered dynamics of forest recovery under a changing climate

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Abstract

Forest regeneration following disturbance is a key ecological process, influencing forest structure and function, species assemblages, and ecosystem–climate interactions. Climate change may alter forest recovery dynamics or even prevent recovery, triggering feedbacks to the climate system, altering regional biodiversity, and affecting the ecosystem services provided by forests. Multiple lines of evidence – including global-scale patterns in forest recovery dynamics; forest responses to experimental manipulation of CO_2, temperature, and precipitation; forest responses to the climate change that has already occurred; ecological theory; and ecosystem and earth system models – all indicate that the dynamics of forest recovery are sensitive to climate. However, synthetic understanding of how atmospheric CO_2 and climate shape trajectories of forest recovery is lacking. Here, we review these separate lines of evidence, which together demonstrate that the dynamics of forest recovery are being impacted by increasing atmospheric CO_2 and changing climate. Rates of forest recovery generally increase with CO_2, temperature, and water availability. Drought reduces growth and live biomass in forests of all ages, having a particularly strong effect on seedling recruitment and survival. Responses of individual trees and whole-forest ecosystems to CO_2 and climate manipulations often vary by age, implying that forests of different ages will respond differently to climate change. Furthermore, species within a community typically exhibit differential responses to CO_2 and climate, and altered community dynamics can have important consequences for ecosystem function. Age- and species-dependent responses provide a mechanism by which climate change may push some forests past critical thresholds such that they fail to recover to their previous state following disturbance. Altered dynamics of forest recovery will result in positive and negative feedbacks to climate change. Future research on this topic and corresponding improvements to earth system models will be a key to understanding the future of forests and their feedbacks to the climate system.

Keywords: biogeochemistry, climate feedback, FACE, irrigation, regime shift, succession, throughfall manipulation, warming

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Introduction

The dynamic process of forest regeneration following disturbance is of key importance, with ramifications on several scales. On a local level, forest recovery involves wholesale rearrangement of vegetative structure, carbon (C) and nutrient cycling, ecosystem physiology, and community structure (Table 1). On a landscape level, disturbance–recovery dynamics play an impor-

tant role in the maintenance of species diversity, as different species use forests of different ages as habitat patches. On a regional to global level, secondary forests are consequential for their role in climate regulation. Forests recovering from disturbance (secondary forests) are strong C sinks and play an important role in the global C cycle (Running, 2008; Pan *et al.*, 2011). For instance, in recent years (2000–2007), regrowth of tropical forests following agricultural abandonment took up an estimated 1.7 Pg C yr^{-1} (Pan *et al.*, 2011), which is equivalent to ca. 20% of annual global fossil fuel emissions. Beyond their influence on climate through their role in the global carbon cycle, secondary forests also influence climate through biophysical mechanisms (Liu

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Table 1 Typical trajectories of change in forest properties following stand-replacing disturbance

Forest property	Typical trajectory	References
Biomass		
Biomass accumulation rate	Rapid initial increase, peak at intermediate age followed by slow decline to near zero in old-growth forests.	Lichstein *et al.*, 2009; Yang *et al.*, 2011; Hember *et al.*, 2012
Leaf biomass or area	Rapid initial increase, relatively stable thereafter.	Uhl & Jordan, 1984; Bormann & Likens, 1994; Law *et al.*, 2003; Goulden *et al.*, 2011; Yang *et al.*, 2011
Fine root biomass	Rapid initial increase, relatively stable or modest decline thereafter.	Vogt *et al.*, 1983; Claus & George, 2005; Yuan & Chen, 2010
Carbon cycle		
Gross primary productivity	Rapid initial increase, relatively stable or modest decline thereafter.	Amiro *et al.*, 2010; Goulden *et al.*, 2011
Net primary productivity	Rapid initial increase, modest decline thereafter.	Gower *et al.*, 1996; Law *et al.*, 2003; Pregitzer & Euskirchen, 2004; Goulden *et al.*, 2011
Heterotrophic respiration	Relatively constant.	Law *et al.*, 2003; Pregitzer & Euskirchen, 2004; Goulden *et al.*, 2011
Net ecosystem C balance	Initially negative (C source), increasing to maximum (C sink) at intermediate ages, declining thereafter. Controversy remains as to whether it declines to zero (C neutrality).	Law *et al.*, 2003; Pregitzer & Euskirchen, 2004; Zhou *et al.*, 2006; Baldocchi, 2008; Luyssaert *et al.*, 2008; Amiro *et al.*, 2010; Goulden *et al.*, 2011
Biogeochemistry		
Foliar [N]	Relatively constant with age, although both decreases (more common) and increases have been observed.	Davidson *et al.*, 2007; Drake *et al.*, 2010; Yang *et al.*, 2011
N mineralization	Mixed responses; both increases and decreases have been observed.	Vitousek *et al.*, 1989; LeDuc & Rothstein, 2010
Hydrology		
Canopy transpiration	Rapid initial increase, modest decline thereafter.	Roberts *et al.*, 2001; Delzon & Loustau, 2005; Amiro *et al.*, 2006; Drake *et al.*, 2011a
Hydraulic limitation	Increases with age.	Drake *et al.*, 2010, 2011a
Sensitivity to variation in water availability	Decreases with age.	McMillan *et al.*, 2008; Drake *et al.*, 2010; Voelker, 2011
Community dynamics		
Species turnover	Rapid initial turnover, decelerating decrease in turnover rate as the forest ages.	Anderson, 2007b
Species richness	Initial increase, sometimes peaking and declining modestly in older forests.	Shafi & Yarranton, 1973; Finegan, 1996; Anderson, 2007b
Competition	Increasing competitive advantage to late-successional species (e.g., shade tolerant, slow growing, higher wood density, longer lived)	Bazzaz, 1979; Bazzaz & Pickett, 1980; Finegan, 1984
Size structure	Initially, relatively even aged; competitive thinning and seedling recruitment drive convergence toward inverse square relationship between abundance and diameter (diverse age structure)	Enquist *et al.*, 2009

et al., 2005; Maness *et al.*, 2012; O'Halloran *et al.*, 2012); for example, in northern regions albedo decreases with forest age and strongly shapes the net climate regulation services of secondary forests (Randerson *et al.*, 2006; Jin *et al.*, 2012; O'Halloran *et al.*, 2012).

A large and growing proportion of forests have been affected by major disturbances. Globally, secondary forests recovering from anthropogenic disturbances such as agriculture and wood harvesting cover an estimated 27 million km^2 (Hurtt *et al.*, 2011), and an estimated 1.2 million km^2 are in use as forestry plantations (Kirilenko & Sedjo, 2007). In addition, natural disturbances affect a significant proportion of Earth's ecosystems; disturbances such as fires, storms, droughts, and insect outbreaks affect over 100 000 km^2 annually in North America alone (Amiro *et al.*, 2010). Climate change is generally increasing the incidence of natural disturbances (Dale *et al.*, 2001), including fires (Westerling *et al.*,

2006) and biotic disturbances such as insect outbreaks (Evangelista *et al.*, 2011; Hicke *et al.*, 2011). Theory and models predict that future climate change may cause even more drastic changes (e.g., Westerling *et al.*, 2011), depending on the future course of greenhouse gas emissions and the resultant shifts in climate (IPCC, 2007). Because secondary forests are strong carbon sinks with considerable value for greenhouse gas mitigation (Anderson-Teixeira & DeLucia, 2011) and also represent a potential bioenergy source (e.g., US DOE, 2011), secondary forests are likely to play substantial roles in climate mitigation initiatives and bioenergy production (Kirilenko & Sedjo, 2007).

Although there is strong and abundant evidence that climate change will affect forests of all ages, we lack synthetic understanding of how climate change will interact with forest age to shape the dynamics of forest recovery. Because forests undergo substantial reorganization of following major disturbance (Table 1), it is likely that climate change will have different effects on forests of different ages, thereby altering the trajectory of succession relative to those observed for historical climates. Climate change may alter one or more distinct features of successional trajectories (Fig. 1). First, the rate at which the forest moves along the successional trajectory may be altered without necessarily implying any changes to the successional pathway or the state of mature forests; for example, increased productivity may accelerate biomass accumulation without altering the biomass of mature forests. Second, the state of mature forests may be altered; for example, maximum biomass may be altered if future climates place differ-

ent biophysical constraints on the number and size of trees that can persist. Third, the successional pathway may be altered; for example, tree establishment may be delayed by altered climatic conditions such that proportionally more time is spent in an early-successional shrub phase. Distinguishing how climate change affects forests of different ages – and thereby how it alters successional trajectories – is critical in understanding how climate change will impact both recently disturbed and mature forests.

This review considers how altered atmospheric CO_2 and climate are likely to impact trajectories of forest recovery, with a particular focus on how climate change may alter the rate of succession, the state of mature forests, and successional pathways (Fig. 1). We consider five major lines of evidence relating forest structure and function to directional variation in CO_2 and climate (i.e., average conditions, as opposed to intra- or interannual variation), each of which yields insight into how forest recovery may be altered under a changing climate. First, we review how climatic influences the dynamics of forest recovery across broad climatic gradients. Second, we summarize the results of experimental studies quantifying the effects of elevated CO_2, elevated temperature, and altered precipitation regimes on the dynamics of forest recovery. Third, we review observations of altered forest recovery under contemporary multivariate environmental change. Fourth, we consider how altered community dynamics may impact forest recovery. Fifth, we review model predictions. Finally, we synthesize findings from these separate lines of evidence, identify remaining uncertainties, and discuss the implications for ecological communities, biogeochemical processes, and the climate system.
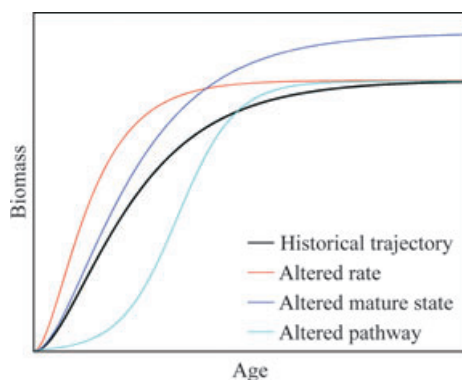
Dynamics of forest recovery across broad climatic gradients

Although few studies have evaluated how climate influences forest recovery across broad climatic gradients (Prach & Rehounková, 2006; Anderson, 2007a), there is clear evidence that climate exerts a strong influence on the rate of succession, the state of mature forests, and their successional pathways (Fig. 1). The rate of forest regrowth following disturbance is strongly influenced by climate (Brown & Lugo, 1982; Johnson *et al.*, 2000; Anderson *et al.*, 2006). Globally, the rate of living biomass accumulation increases with temperature, being on average three to four times faster in the tropics than in high-latitude forests (Fig. 2a; Anderson *et al.*, 2006). Likewise, biomass accumulation rate increases with precipitation at a global scale (Fig 2b). Within the tropics, rates of biomass accumulation are

Fig. 1 Schematic diagram illustrating three ways in which climate change may impact the dynamics of forest recovery. Relative to the historical trajectory of change in a forest property (here, biomass) with age, climate change may alter (1) the rate of change, (2) the state to which the property converges as the forest matures ('mature state'), or (3) the successional pathway (i.e., the sequence of states through which any given ecosystem property passes and the relative amount of time spent in each).
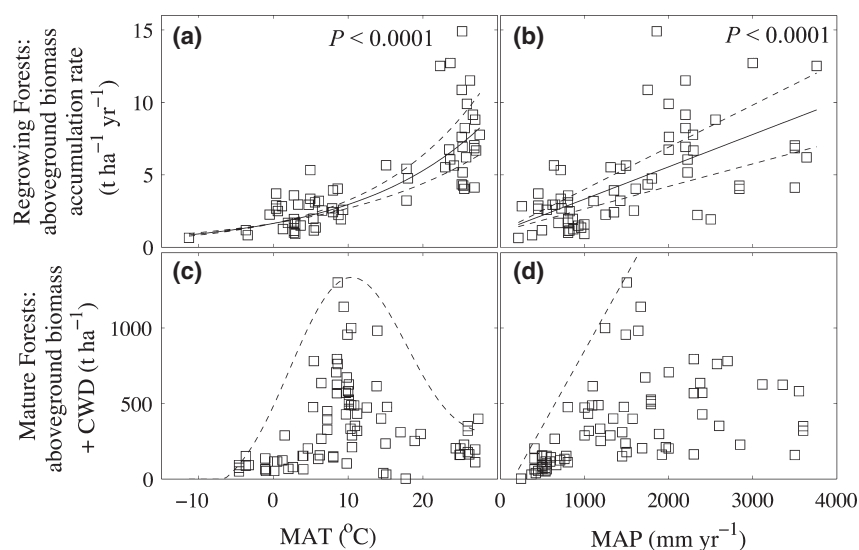
Fig. 2 Influence of climate on forest recovery rates (a, b) and on aboveground C stocks of mature forests (c, d). The rate of aboveground biomass accumulation in forests recovering from stand-clearing disturbance varies globally with respect to (a) mean annual temperature (MAT) and (b) precipitation (MAP). Data, which are from Anderson *et al.* (2006), represent natural regeneration in 68 unmanaged forests worldwide. Solid and dashed lines represent an exponential fit and its 95% confidence interval, respectively. Similarly, aboveground C stocks (biomass + coarse woody debris; CWD) in mature forests vary globally with respect to (c) MAT and (d) MAP. Data from Anderson-Teixeira *et al.* (2011). Dashed lines represent hypothesized bioclimatic limits.

dramatically higher in moist climates (precipitation 1000–2500 mm yr^{-1}) than in dry climates (precipitation <1000 mm yr^{-1}); however, the positive influence of precipitation appears to saturate, with rates in wet climates (precipitation >2500 mm yr^{-1}) less than or equal to those in moist climates (Brown & Lugo, 1982; Marín-Spiotta *et al.*, 2008). Although further research is required to fully understand the mechanisms through which temperature, water availability, and their seasonal dynamics affect rates of biomass accumulation in secondary forests, we can say conclusively that warmer temperatures and higher moisture availability are associated with higher rates of biomass accumulation.

Growth in secondary forests is strongly linked to elemental cycling. Biogeochemical cycles of elements including C, nitrogen (N), and phosphorous (P) are coupled to biomass accumulation through stoichiometric constraints on the elemental composition of vegetation, such that rates at which these elements are sequestered in vegetation are grossly proportional to rates of biomass accumulation (Yang *et al.*, 2011). Indeed, mirroring the climate dependence of rates of biomass accumulation (Fig. 2a–b; Anderson *et al.*, 2006), it has been observed that the rate of N uptake by a regrowing tropical forest in Costa Rica is four times that of a regrowing temperate forest at Hubbard Brook, USA (Russell & Raich, 2012). However, the trajectory of forest recovery is also shaped by biogeochemistry–climate interactions. For example, climate influences

temporal patterns of N availability during secondary succession (Vitousek *et al.*, 1989), rates of change in soil C and N (Li *et al.*, 2012), and plant tissue stoichiometry (Wright *et al.*, 2004). Thus, climate may indirectly influence forest recovery through its influence on biogeochemistry, as occurs in the case of forests developing on Hawaiian lava flows (Anderson-Teixeira *et al.*, 2008; Anderson-Teixeira & Vitousek, 2012).

A few studies have compared rates or pathways of secondary succession across broad climatic gradients. Following clear cutting in western Oregon, climate shapes both the rate and pathway of forest succession; in the western Cascades region, conifer regeneration is slower and follows a longer establishment delay compared with the more mesic Coastal Range region (Yang *et al.*, 2005). In subalpine forests of the Colorado Rockies, the rate of succession is more than twice as rapid in mesic sites as compared with xeric sites (Donnegan & Rebertus, 1999). Likewise, in the Medicine Bow mountains of Wyoming, succession to a mature spruce–fir forest is most rapid in a mesic drainage bottom, slower on a less mesic north-facing slope, and rarely occurs at more arid sites prior to stand-clearing fire (Romme & Knight, 1981). In the Czech Republic, the rate of succession in vegetative communities (including forests and nonforests) is strongly influenced by climate; mean annual change in dominant species cover during the first 12 years of succession decreases dramatically with increasing elevation (increasing precipitation and

decreasing temperature; Prach *et al.*, 2007). These examples provide evidence that climate strongly influences both the rate and pathway of succession.

In addition to its influence on the rate and trajectory of forest recovery, climate also shapes the types of steady-state conditions toward which secondary forests can eventually converge. Globally, aboveground biomass of forests is influenced by temperature and precipitation (Fig. 2c–d; Keith *et al.*, 2009; Anderson-Teixeira *et al.*, 2011; Larjavaara & Muller-Landau, 2012), and climate strongly influences most other major components of ecosystem C cycles, including gross and net primary productivity (GPP and NPP, respectively; Luyssaert *et al.*, 2007), soil and whole-ecosystem respiration, and soil organic carbon (Raich & Schlesinger, 1992; Jobbágy & Jackson, 2000). Similarly, species diversity varies globally with respect to climate (Brown *et al.*, 1998). In sum, climate can determine the state to which forests converge following disturbance both directly through biophysical constraints and indirectly through its influence on biogeochemistry and the surrounding metacommunity.

The broad-scale patterns described above demonstrate that climate strongly influences the rate of forest recovery, successional pathways, and the structure and function of mature forests. However, transient dynamics under a rapidly changing climate may diverge from expectations based on these contemporary patterns, and increasing atmospheric CO_2 concentrations will alter physiological constraints on forests. To understand the more immediate responses of forest recovery to elevated CO_2 and climate change, we turn to experimental manipulations.

Forest responses to experimental manipulation of CO_2, temperature, and precipitation

Experiments manipulating CO_2, temperature, and precipitation demonstrate that altered climatic conditions will alter ecosystem and community dynamics in secondary forests. The responses of terrestrial ecosystems in general to these experimental manipulations have been previously reviewed (e.g., Pendall *et al.*, 2004; De Graaff *et al.*, 2006; Norby & Zak, 2011; Wu *et al.*, 2011; Beier *et al.*, 2012; Dieleman *et al.*, 2012; Lu *et al.*, 2012); here, we focus specifically on the responses of forests and any age dependency of their responses (Fig. 3).

Responses to CO_2 fertilization

Tree-dominated ecosystems – all in temperate or boreal regions – have been exposed to elevated CO_2 through Free-Air Carbon dioxide Enrichment (FACE), Open Top Chamber (OTC), and Whole Tree Chamber (WTC) experiments. Given the logistical difficulties of elevating CO_2 in forests with tall canopies, the majority of these experiments have been performed on young forests or trees, with only one FACE experiment in a mature forest to date (Table S1).

Elevated CO_2 consistently enhances photosynthesis, or GPP at the ecosystem level (Ceulemans & Mousseau, 1994; Curtis & Wang, 1998; Ainsworth & Long, 2005; Hyvönen *et al.*, 2007). In young forests, this results in increased NPP and biomass; at least at the onset of the experiment (DeLucia *et al.*, 1999; Norby *et al.*, 2005). However, whereas substantial NPP and biomass increases have occurred at the onset of experiments, this NPP stimulation has persisted in some but not all forests (Oren *et al.*, 2001; Seiler *et al.*, 2009; McCarthy *et al.*, 2010; Norby *et al.*, 2010). Moreover, this response becomes less consistent as forests become older, and NPP did not increase in the only mature forest exposed to elevated CO_2 (Fig. 3; Körner *et al.*, 2005; Bader *et al.*, 2009). Similarly, leaf and fine root biomass are consistently stimulated in young forests, but may decline in old forests (Fig. 3; Körner *et al.*, 2005; Bader *et al.*, 2009). Thus, although there is strong evidence that CO_2 fertilization increases the rate of biomass accrual in young forests, a question remains as to whether elevated CO_2 increases the biomass and productivity of mature forests (Fig. 1; Körner *et al.*, 2005; Hyvönen *et al.*, 2007; Norby & Zak, 2011). In large part because of this uncertainty, it remains unclear whether the net carbon balance of mature forests will increase in response to CO_2 fertilization (Fig. 3).

The ability of forests to sustain increased NPP under elevated CO_2 as they age – and, ultimately, the potential for mature forests to increase C storage under elevated CO_2 – depends in large part upon biogeochemistry. One potential explanation of observed declines in NPP stimulation under elevated CO_2 as forests age is that increased productivity immobilizes nutrients in woody tissue or soil organic matter such that soil N and other nutrients needed to sustain growth become depleted and may eventually limit growth (Luo *et al.*, 2004). Progressive N limitation can be alleviated through a variety of mechanisms: trees can increase their N use efficiency, invest more C in belowground nutrient acquisition, or access deep N pools (McKinley *et al.*, 2009; Iversen, 2010; Drake *et al.*, 2011b; Norby & Zak, 2011). N limitation can also be mitigated if greater N mineralization occurs under high CO_2, or if N_2 fixation is stimulated by elevated CO_2 (Zanetti *et al.*, 1996; Hungate *et al.*, 2004; Luo *et al.*, 2004; Hoosbeek *et al.*, 2011; Norby & Zak, 2011). Early work suggested that N mineralization declines under elevated CO_2 (Hungate *et al.*, 1999), but more recent studies suggest that there can be a priming effect through time from increased atmospheric CO_2 that stimulates soil micro-
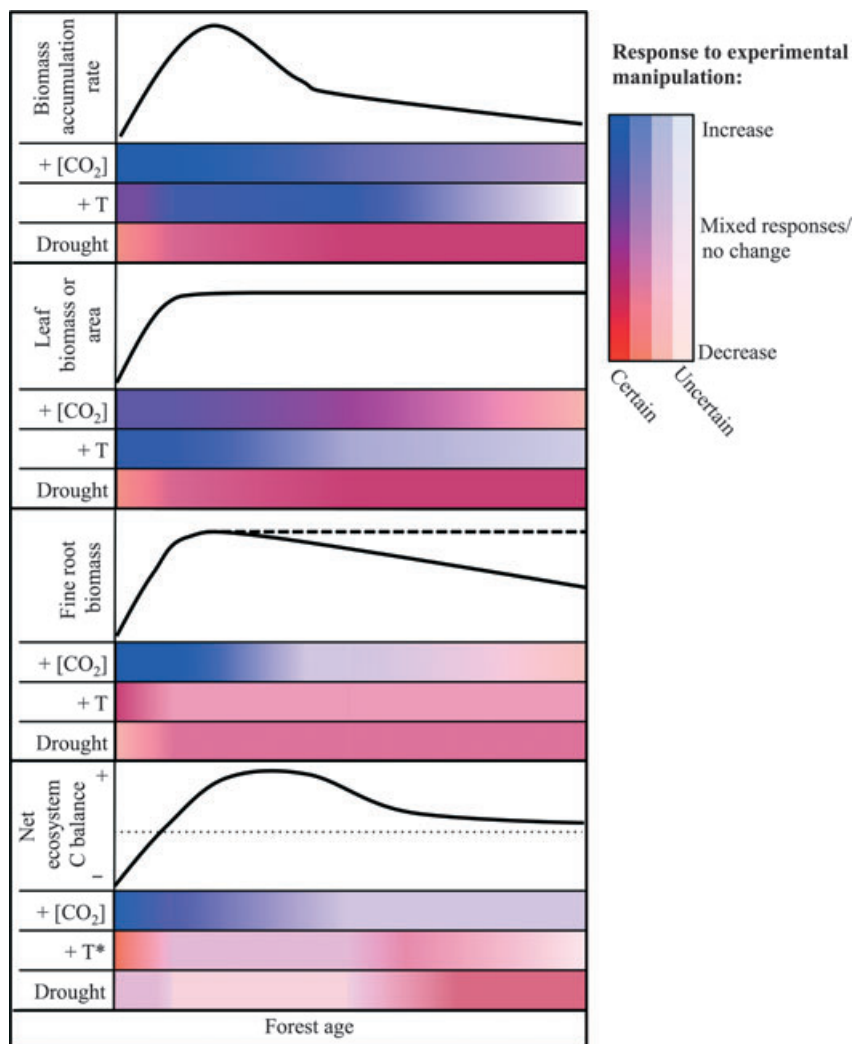
Fig 3 Schematic diagram illustrating typical forest successional trajectories under ambient climate (solid lines; as reviewed in Table 1) and how these are affected by experimental CO_2 fertilization, warming, and drought (increases in blue, decreases in red; color saturation scales with certainty). Responses to CO_2 and climate change are based on a comprehensive review of experimental studies (Tables S1–S3). Responses are considered to have high certainty when observed in multiple sites and low certainty when observed in only one study. *Indicates a response that is time dependent; it may change from negative to positive as increased N mineralization stimulates biomass growth (Melillo *et al.*, 2011).

bial activity, which in turn degrades slowly cycling organic matter pools and release mineral N (Carney *et al.*, 2007; Langley *et al.*, 2009; Drake *et al.*, 2011b). Elevated CO_2 may also increase N availability by increasing labile C to drive the energetics of N_2 fixation (Hungate *et al.*, 1999). However, in a scrub-oak system in Florida, N_2 fixation was negatively impacted by 7 years exposure to elevated CO_2 (Hungate *et al.*, 2004), and N_2-fixation rates have continued to decline – perhaps due to canopy closure and light limitation (Duval, 2010). Thus, N deficiency may be avoided – and NPP stimulation sustained – over time through a variety of mechanisms; however, it remains

uncertain whether this can continue indefinitely or whether NPP stimulation in all forests would eventually decline given sufficient time (Hyvönen *et al.*, 2007; Norby & Zak, 2011).

The responses of tree growth to elevated CO_2 are variable among species (Bazzaz, 1990; Saxe *et al.*, 1998; Peñuelas *et al.*, 2001; Körner *et al.*, 2005; Seiler *et al.*, 2009; Dawes *et al.*, 2011), and differential species responses have commonly been observed in CO_2-enrichment experiments (Table S1). For example, of the three codominant canopy tree species (*Fagus sylvatica*, *Quercus petraea*, *Carpinus betulus*) in the mature deciduous forest exposed to elevated

CO_2, shade-tolerant *Fagus* exhibited increased annual basal area increments in response to CO_2 in two of four treatment years, whereas growth of the other species remained the same or declined (Körner *et al.*, 2005). Similarly, proportional species' contributions to whole-ecosystem productivity shifted in a Florida scrub–oak ecosystems exposed to elevated CO_2: dominant *Quercus myrtifolia* exhibited strong biomass growth, *Q. chapmanii* exhibited less of an effect, and subdominant *Q. geminata* showed no growth stimulation (Dijkstra *et al.*, 2002). Thus, differential species growth responses consistently alter proportional species' contributions to whole-ecosystem productivity and will likely change the composition of future communities.

Understory vegetation can influence ecosystem functioning and future community composition (Nilsson & Wardle, 2005) and, therefore, impacts of global change on juvenile trees and influential nontree species serve as a window into the forests of the future. Moreover, as the majority of forest biodiversity is in the understory stratum, impacts on understory species as well as symbiotic mycorrhizal fungi bear consequences for tree recruitment, carbon cycling, forest health and biodiversity (Gilliam, 2007). Understory community responses to CO_2 enrichment have been commonly observed (Table S1). At ORNL-FACE, the woody understory increased in importance relative to the total stand and to herbaceous plants, indicating a potential acceleration of succession under elevated CO_2 (Souza *et al.*, 2010). Consistent with earlier work using pots and growth chambers (Bazzaz & Miao, 1993; Kubiske & Pregitzer, 1996; Kerstiens, 1998, 2001; Hättenschwiler & Körner, 2000), CO_2 enrichment at DukeFACE tended to favor slow-growing, shade-tolerant species with low rates of productivity in understory conditions, again suggesting that succession may be accelerated in temperate forests under future conditions, with implications for biosphere–atmosphere carbon feedbacks (Mohan *et al.*, 2007). In addition, CO_2 enrichment may favor woody vines (lianas; e.g., Sasek & Strain, 1990). This has been observed in two FACE studies (Table S1); for example, at DukeFACE, the woody vine poison ivy (*Toxicodendron radicans*) growth was disproportionately enhanced under elevated CO_2 (Mohan *et al.*, 2006). Lianas have been expanding in abundance in many regions of the world – often to the detriment of recruiting and mature trees (Dillenburg *et al.*, 1995; Ingwell *et al.*, 2010; Schnitzer & Carson, 2010; Schnitzer & Bongers, 2011) – and the positive feedback of elevated CO_2 for vines may hinder the establishment of secondary forests globally. Thus, increasing atmospheric CO_2 may substantially alter the rate and pathway of succession as well as the composition of mature forest communities (Fig. 1).

Responses to warming

Over the last three decades, several tree-dominated ecosystems of various ages – almost all in temperate and boreal regions – have been exposed to experimental warming (Table S2). These experiments have warmed either aboveground vegetation or the soil (through use of buried cables); there are few soil-and-air warming experiments done at the scale of canopy trees (Slaney *et al.*, 2007; Bronson & Gower, 2010).

Soil warming in northern forests results in faster decomposition and microbial processing of soil C and N, which directly releases more CO_2 to the atmosphere because of enhanced soil respiration (Table S2; Rustad *et al.*, 2001; Melillo *et al.*, 2002, 2011). By increasing N mineralization rates, soil warming can have an indirect N fertilization effect, which generally increases aboveground production and lowers C allocation to fine root biomass (Fig. 3; Zhou *et al.*, 2011). The net ecosystem C balance in response to warming depends largely on the counteracting effects of C release through increased soil respiration and C sequestration through increased biomass growth (Fig. 3); in a 60- to 70-year-old even-aged oak–maple forest in central Massachusetts subjected to 7 years of soil warming (Harvard Forest), soil C losses were increasingly offset by stimulated growth of canopy trees (after a lag of several years; Melillo *et al.*, 2011; Butler *et al.*, 2012). Additional changes may be driven by aboveground warming; over the first few years of warming in a 12-year-old black spruce (*Picea mariana*) plantation in Manitoba, soil respiration increased under soil warming but decreased under soil-and-air warming (Bronson *et al.*, 2008). In this study, elevated soil and air temperatures increased spruce tree shoot growth (Bronson *et al.*, 2009) but did not change rates of photosynthesis or autotrophic respiration (Bronson & Gower, 2010). Much remains to be learned about how warming affects whole forested ecosystems, particularly in subtropical and tropical forests, where only one warming experiment has been conducted to date (Cheesman & Winter, 2012). Moreover, although we may posit that forest age modulates warming responses based on the magnitude of structural and functional changes associated with forest recovery (Table 1), there is of yet no clear evidence that the direction of forest responses to warming varies by age (Fig. 3).

Growth responses to warming vary among tree species (Table S2), and this is likely to affect successional dynamics and forest composition. For example, although the large oaks at Harvard forest accounted for the majority of C uptake and storage in woody tissue, smaller maples exhibited a greater stimulation of growth in response to soil warming stimulation (Mel-

illo *et al.*, 2011; Butler *et al.*, 2012; Mohan *et al.*, unpublished results). Similarly, a warming experiment in a recently timbered oak–hickory forest in Pennsylvania found altered phenology (with differential responses among species) and community composition (Rollinson, 2010; Rollinson & Kaye, 2011). Thus, warming is likely to alter species' growth and phenology and, thereby, the rate and pathway of succession and ultimately the community composition of mature forests (Fig. 1).

Responses to altered precipitation

There have been a number of precipitation manipulation experiments in forests of a range of ages spanning from boreal to tropical regions (Table S3; Beier *et al.*, 2012). Across this range of climates and forest ages, tree growth and survival were generally increased by water addition and reduced by water removal (Fig. 3; e.g., Hanson *et al.*, 2001; Nepstad *et al.*, 2002; Plaut *et al.*, 2012; Vasconcelos *et al.* (2012), as was GPP or NPP at the ecosystem level (Nepstad *et al.*, 2002; Alberti *et al.*, 2007). Soil respiration rates also tended to increase under irrigation and decrease under drought (Table S3; e.g., Conant *et al.*, 2000; Sotta *et al.*, 2007). However, water addition only accelerated forest C cycling up to a point; some more mesic forests did not respond to precipitation manipulation (De Visser *et al.*, 1994; Bergh *et al.*, 1999) or had accelerated C cycling under reduced precipitation (Cleveland *et al.*, 2010). Sensitivity to precipitation manipulation often varied by size class, but results were mixed as to whether small or large trees were more sensitive (Hanson *et al.*, 2001; Nepstad *et al.*, 2007). Whereas altered precipitation had a strong effect on seedling emergence and survival (Richter *et al.*, 2012; Volder *et al.*, 2012) and at times had a stronger effect on small than on large trees (Hanson *et al.*, 2001), there were also instances where exposed canopy trees suffered greater drought-related stress (Nepstad *et al.*, 2007; Schuldt *et al.*, 2011). Thus, within-stand relationships between tree age and drought sensitivity do not necessarily mirror across-stand relationships, where growth sensitivity to variation in water availability declines with stand age (Table 1). As with experimental manipulation of CO_2 and temperature, differential species responses were commonly observed under precipitation manipulation experiments (Table S3; e.g., Yavitt & Wright, 2008), portending future changes to community composition under altered precipitation regimes. Thus, in summary, precipitation manipulation experiments have demonstrated that water availability affects rates of forest recovery, mature forest states, and probably successional pathways (Figs 1 and 3).

Responses to multivariate environmental manipulation

Joint effects of altered CO_2, temperature, and precipitation are rarely purely additive (Dieleman *et al.*, 2012), and understanding the interactive effects produced by combined manipulations remains an important challenge. Experimental manipulation of more than one of these elements in a factorial design has occurred in several intact forests or experimental mesocosms (Tables S1–S3). These studies demonstrate that tree growth and carbon cycling in young forests are generally accelerated under combined higher CO_2, warmer, and wetter conditions (Tables S1–S3; e.g., Wan *et al.*, 2004; Comstedt *et al.*, 2006; Slaney *et al.*, 2007; Tingey *et al.*, 2007; Bauweraerts *et al.*, 2013). In addition, different species have responded differently to different elements of climate change; for example, at the alpine tree line in Switzerland, growth of *Larix decidual* responded positively to CO_2 but was unresponsive to soil warming, whereas *Pinus cembra* had a slight positive response to warming but responded minimally to CO_2 (Dawes *et al.*, 2011). The limited number of studies and the complexity of multifactor experiments make it premature to generalize about how forests of different ages will respond to interactive elements of global change. However, observed responses of forests to the environmental change that has already occurred – to which we turn next – reveal how secondary forests are responding to multivariate climate change to date.

Altered forest recovery under contemporary multivariate environmental change

Historical reconstructions indicate that forests of all ages have responded to the changes in CO_2 and climate that have already occurred. By nature, these historical records do not directly separate the effects of CO_2, temperature, and precipitation from one another and from other potentially confounding environmental changes (e.g., atmospheric deposition, ozone, management, altered disturbance regimes). Rather, they provide a picture of how the dynamics of forest recovery are responding to contemporary multivariate environmental change.

Tree-ring and observational records extending back decades to centuries have demonstrated the climate dependence of forest productivity. Tree-ring records have revealed increasing growth rates in numerous forests including high-elevation forests in western Washington (Graumlich *et al.*, 1989), conifers in the white mountains of California (Lamarche *et al.*, 1984; Salzer *et al.*, 2009), *Pinus ponderosa* forests in the US Pacific northwest (Soulé & Knapp, 2006), aspen (*Populus tremuloides*) secondary forests in Wisconsin (Cole

et al., 2010), *Abies* and *Quercus* forests in France (Becker, 1989; Becker *et al.*, 1994), and numerous other forests throughout Europe (Spiecker, 1999; Babst *et al.*, 2013). These increased growth rates are generally attributable to increased atmospheric CO_2, temperature, or moisture (e.g., Graumlich *et al.*, 1989; Soulé & Knapp, 2006; Salzer *et al.*, 2009; Cole *et al.*, 2010). In contrast, tree growth rates have decreased in response to warming or drought stress in many other forests around the world (Allen *et al.*, 2010), including white spruce (*Picea glauca*) in interior Alaska (Barber *et al.*, 2000), conifers in the southwest United States (Williams *et al.*, 2013), and tropical forests in Panama, Malaysia, and Costa Rica (Feeley *et al.*, 2007b; Clark *et al.*, 2010). Similarly, a review documenting evidence of altered forest productivity over the last half century indicates that the productivity of many forests is increasing whereas that of others is declining (Boisvenue & Running, 2006). Although powerful for understanding the historical influence of climate on forest productivity, these records are limited in that they do not characterize responses across a range of forest ages.

By comparing biomass–age relationships (determined through a chronosequence approach) with current biomass accumulation rates in forests of various ages (determined through repeated sampling), a couple of studies have identified accelerated biomass accumulation in forests following stand-clearing disturbances. Specifically, accelerated biomass accumulation has been observed in temperate deciduous forests in the eastern United States (McMahon *et al.*, 2010a; see also Foster *et al.*, 2010; McMahon *et al.*, 2010b) and in temperate-maritime forests in the Pacific northwest (Fig. 4; Hember *et al.*, 2012). Likely explanations of these increases in secondary forest biomass accumulation rates include increased atmospheric CO_2, increased temperature, increased moisture, and increased growing season length (McMahon *et al.*, 2010a; Hember *et al.*, 2012). Thus, climate change appears to be increasing the rate of forest regrowth in some temperate forests; however, parallel studies have yet to be conducted in other regions.

The long time frame of forest recovery precludes comparison of forests that have matured under different climates, which would be necessary to determine whether climate change is altering recovery trajectories such that forests converge to an altered state as they mature (Fig. 1). However, long-term monitoring of mature forests can provide evidence as to whether climate change is affecting the state of forests that matured under past climates. Long-term monitoring of old-growth forests provides mixed evidence as to whether their total carbon storage capacity is changing;
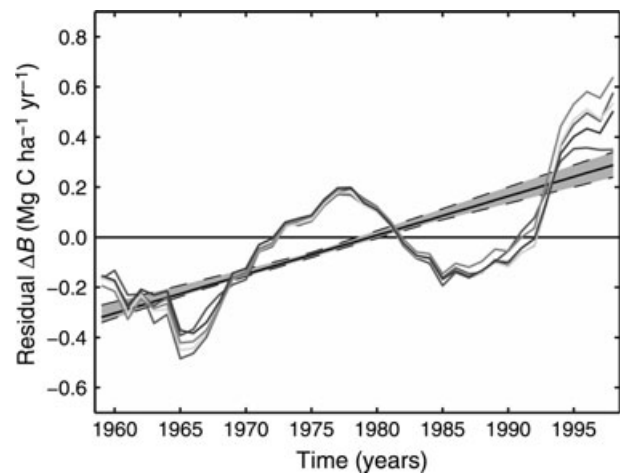

Fig. 4 Evidence of increasing rates of biomass accumulation in coastal Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) forests in southwest British Columbia, Canada. Plotted is the residual average biomass increment (ΔB) from 1267 permanent inventory plots after correction for factors including stand age, site quality, nitrogen availability, and biomass (the five lines represent different correction methods, as detailed in Hember *et al.*, 2012). Linear regression represents a significant positive trend. Reprinted from Hember *et al.* (2012).

many old-growth forests throughout the world appear to be net C sinks (Baker *et al.*, 2004; Luyssaert *et al.*, 2007; Chave *et al.*, 2008; Lewis *et al.*, 2009); however, this effect is diminished at larger spatiotemporal scales of measurement (Clark, 2002; Feeley *et al.*, 2007a; Chave *et al.*, 2008). There is strong evidence of directional change in community composition of forests throughout the world; for example, long-term records from the 50 ha forest dynamics plot on Barro Colorado Island, Panama, indicate increased dominance of drought-tolerant species (Feeley *et al.*, 2011). In addition, there have been general increases in forest die-back globally – a phenomenon attributed to climate change–type drought (Breshears *et al.*, 2005; Allen *et al.*, 2010; Williams *et al.*, 2013).

Thus, there is evidence of historical change in both rates of forest regrowth and the state of forests that matured under past climates. There is also some evidence of changing successional trajectories driven by altered community dynamics (reviewed below). Although concurrent changes in multiple environmental factors including atmospheric CO_2, climate, atmospheric deposition, herbivore communities, disturbance regimes, and management make it difficult to isolate the cause of these changes, their global distribution and directional correlation with trends in CO_2 and climate provide strong evidence that they are at least partially attributable to increasing atmospheric CO_2 and climate change.

Community dynamics and the potential for state changes

Successional pathways may be altered when elevated CO_2 and climate change affect community dynamics, either directly through differential effects on the performance of various species and size classes or indirectly through altered disturbance regimes and consequent competitive outcomes.

Climate change will alter community dynamics by altering the physical environment in which species of varying physiological strategies are competing. Experimental climate change manipulations (reviewed above; Tables S1–S3) and decades of forestry research on the climate sensitivity of forest regeneration (Fowells & Stark, 1965; Ferrell & Woodard, 1966; Thomas & Wein, 1985) have demonstrated that increased CO_2 and altered climate will differentially affect growth rates of trees by size and species, thereby altering population dynamics, competitive interactions, and species composition of both young and mature forests. In addition, climate change can differentially favor or inhibit common forest pathogens, providing another mechanism of impact on community structure (reviewed by Sturrock *et al.*, 2011). Such community changes can affect ecosystem function, altering production, C stocks, and biogeochemistry. For example, model predictions of climate change effects on forest productivity can be very different if the community is allowed to develop dynamically, compared with using parameters based on average forest characteristics, which is a common practice in biogeochemical models examining the effects of climate change (Bolker *et al.*, 1995).

Beyond its direct effects on the dynamics of forest recovery through physiological mechanisms, climate change may also impact successional pathways indirectly by altering the frequency, timing, severity, and spatial extent of disturbances including fires, droughts, storms, floods, and herbivore or pathogen outbreaks (e.g., Dale *et al.*, 2001; Westerling *et al.*, 2006; Allen *et al.*, 2010; Sturrock *et al.*, 2011). Frequency and intensity of disturbance have been theoretically shown to have very different effects on community diversity (Miller *et al.*, 2011; in determining microcosm diversity (Hall *et al.*, 2012). Thus, changes in disturbance frequency and intensity have the potential to shift community composition, even when species are restricted to (and are still viable in) their historic ranges. Moreover, large changes to disturbance regimes are not required to facilitate changes in community composition; in the annual plant model of Miller *et al.* (2011), changing disturbance mortality by just a few percentage points can send a species to extinction. Changes in community composition driven by altered disturbance regimes

may have dramatic consequences for ecosystem functioning. For example, in Alaskan boreal forests, increasing fire frequency and severity have shifted competitive dominance from conifers to deciduous species, affecting biomass and soil C accumulation, albedo, and energy partitioning (Beck *et al.*, 2011).

Disturbance can also provide niche opportunities for invaders (Shea & Chesson, 2002), and the successful invasion can dramatically alter successional trajectories and also feedback to further modify disturbance regimes (Mack & D'Antonio, 1998). Although disturbances are commonly believed to increase invader success, recent work suggests that it is changes to disturbance regimes, rather than disturbance events *per se* that most strongly influence a communities' susceptibility to invasions (Moles *et al.*, 2012). In this light, climate change is likely to change the composition of some communities by altering disturbance regimes to a point where invader species can become dominant.

In some cases, climate change may push forests past critical thresholds such that, upon perturbation, they undergo drastic changes in community composition and ecosystem properties ('catastrophic shift') and fail to return to their previous state (Fig. 5). In many systems, the observed state of the community is not the only possible stable state; a variety of empirical results demonstrate the existence of alternative stable states in nature (D'Antonio & Vitousek, 1992; Savage & Mast, 2005; Schröder *et al.*, 2005; Odion *et al.*, 2010; Scheffer *et al.*, 2012). Large changes in the environment can bring about large changes in ecosystems, but smooth, gradual changes in abiotic conditions also can cause abrupt shifts in ecosystem properties and functioning (Scheffer *et al.*, 2001). Systems that are structured by disturbance and are susceptible to abiotic forcing (such as regenerating forests) may be more likely to display alternative stable states (Didham *et al.*, 2005). When disturbance keeps systems in perpetual flux, as is the case for many forests, no true stable equilibrium (in the classical, dynamical systems sense) is reached. Instead, forests undergo periodic cycles of disturbance and regeneration, and it is these cycles that constitute the 'state' of the system.

Many forests are resilient (*sensu* Grimm & Wissel, 1997) to commonly experienced disturbances, but effects of climate change, such as changes to the disturbance and precipitation regimes, can change the composition and productivity of forest communities (Thompson *et al.*, 2009), forcing the system into different cyclical behaviors. Although different initial trajectories can lead to different mature forest states, there is also the possibility that different initial trajectories can lead to the same mature state, or that similar initial trajectories can lead to distinct mature states
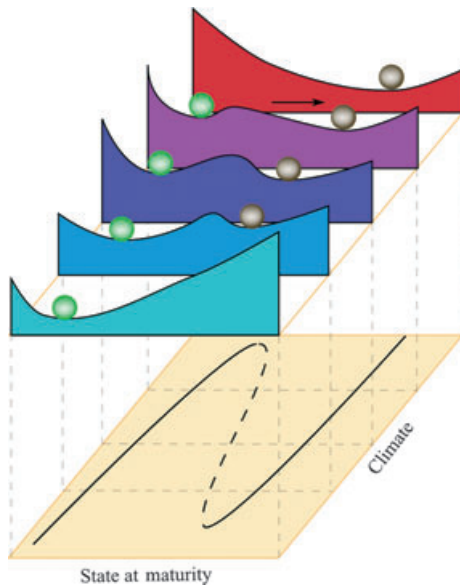
Fig. 5 Schematic diagram illustrating the potential for disturbance to force ecosystems from one stable state to another as the climate changes. Colored shapes represent the landscape of stable ecosystem states under different climate regimes, and balls represent states in which ecosystems can stably exist – in this case, the state to which the system converges at maturity (which will be associated with a stable disturbance–recovery regime). The plot below illustrates hysteresis, wherein alternate stable states exist. As the climate changes, basins of attraction shift such that the stable state at maturity eventually switches from one state to the other. During the transition, however, disturbance (indicated by black arrow) may hasten the shift from one stable state to another. Modified from Scheffer *et al.* (2001).

(Fig. 1, 'alternative transient states' *sensu* Fukami & Nakajima, 2011).

In some forested regions, the existence of alternative stable states implies that forests may not return to their previous state following disturbance. A general mechanism underlying such alternative stable states is that seedlings and young forests are often more vulnerable to disturbances such as drought, herbivory, and fire than their mature counterparts (Table 1; Stromayer & Warren, 1997; Thompson & Spies, 2010). As a result, conditions that support the persistence of mature forests may not be amenable to forest regeneration. For example, following fire, conifer regeneration may be delayed or prevented by drought or competitive inhibition by grasses or shrubs (Savage & Mast, 2005; Roccaforte *et al.*, 2012). There are also systems in which postfire establishment of pyrogenic vegetation or vulnerability of young stands to crown fire reduces the probability of forest regeneration (D'Antonio & Vitousek, 1992; Savage & Mast, 2005; Thompson & Spies, 2010; Staver *et al.*, 2011). For example, in the Klamath region

of Oregon and California, high-intensity fire shifts the community from a high-biomass mixed conifer forest to a pyrogenic low-biomass shrub–chaparral–hardwood community, in which state it may be maintained by subsequent fires of any intensity (Odion *et al.*, 2010; Thompson & Spies, 2010). Alternative stable states may also be driven by hydrologic, microclimatic, or biogeochemical mechanisms; for example, postfire forest resilience may be impacted by changes to soil biogeochemistry and hydrological functioning (Ffolliott *et al.*, 2011; Smithwick, 2011).

Climate change may gradually alter the landscape of alternative states, having minimal impact on mature forests, but shifting conditions such that forests will be unlikely to reestablish following disturbance (Fig. 5). The probability of forest regeneration may be reduced by mechanisms such as reduced probabilities of seedling establishment under more arid conditions, reduced competitive advantage of seedlings relative to grasses or shrubs, or increases in disturbance frequency or severity. Although ecological theory points toward the risk that some forests may unlikely to return to their previous state following stand-clearing disturbance as a result of global change (Fig. 5), empirical evidence remains scant. In the southwestern United States, ponderosa pine forests meet the criteria for forests that may be vulnerable to climate change-induced catastrophic shifts and are often failing to reestablish following fire (Dore *et al.*, 2008; Roccaforte *et al.*, 2012); however, a climate change mechanism has not been demonstrated. Understanding the potential for climate change to dramatically alter or prevent postdisturbance recovery remains an important challenge.

Thus, based on empirical findings and theoretical concepts, community composition and ecosystem function of regenerating forests under climate change are likely to change, both quantitatively, and in terms of stability. Given that climate change, disturbance regimes, and community dynamics interact in complex ways to shape ecosystems, correctly predicting the behavior of forests over the next century will require greater understanding of the potential for altered community dynamics to dramatically impact carbon cycling, biogeochemistry, and ecosystem–atmosphere exchanges.

Ecosystem and earth system model projections

Ecosystem and earth system models (ESMs) provide a means to project dynamically how ecosystems will be impacted by multiple interacting environmental changes over spatiotemporal scales that exceed the limits of observation and experimentation. ESMs vary in complexity from fully coupled global circulation

models (GCMs), which include two-way feedbacks between the land, atmosphere, and oceans to make predictions about climate, to simpler models with less interaction between the earth system components (e.g., one-way feedbacks to the atmosphere such as land-cover changes to net terrestrial CO_2 uptake). ESMs include land components embedded with physiological and biogeochemical mechanistic representations of the interactions between vegetation, the atmosphere, and either prognostic disturbances (i.e., fire) or prescribed disturbances (i.e., harvest). Vegetation is represented in terms of broadly defined plant functional types (PFTs; e.g., temperate conifers). When coupled with a specific class of ecosystem models (dynamic global vegetation models; DGVMs), processes are included that allow vegetation type to change based on climate conditions (e.g., forest to grassland or woodland). Recent advancements to some ESMs (CESM/CLM4.0, ORCHIDEE, TEM) now include dynamic response variables for the long-term physiological changes related to CO_2 and/or temperature (Krinner *et al.*, 2005; Thornton *et al.*, 2007; Zaehle & Friend, 2010). The complexity of these models, and the variety of factors upon which model predictions and associated uncertainty depend, preclude the possibility of any one model incorporating all of the known complexity of forest regeneration. However, for models to make predictions about forest recovery following disturbance, they need to be able to capture the interactive effects of changing environmental conditions and disturbance on forest recovery dynamics.

No model pays detailed attention to the roles of forest age and successional changes in species composition in shaping the dynamics of forest recovery. Rather, regenerating forests are generally parameterized as mature forests, although sometimes there are two age classes (e.g., fire BGC; Smithwick *et al.*, 2009), and carbon allocation to wood may vary dynamically with age (e.g., CLM4; Hudiburg *et al.*, 2013). We are aware of only one model where C allocation to nonwoody components or physiology changes dynamically with age (and this improves performance in describing age trajectories of woody productivity; Davi *et al.*, 2009). Changes in community composition (i.e., PFTs), physiological differences between early- and late- successional species, and age structure within a forest (Table 1) generally are not incorporated (exception is ED2; Medvigy *et al.*, 2009). As a result, models have difficulty accurately reproducing trajectories of change in biomass or other components of the C cycle associated with forest age (Table 1). Nevertheless, to the extent that forest responses are consistent across age classes (Fig. 3), models can predict productivity responses of young forests to elevated CO_2 and climate change. Simulated climate change effects on forest

growth vary by model, region, and climate change scenario; the direction of change in forest growth is expected to vary regionally and to depend on the course of atmospheric CO_2 and climate change (Kirilenko & Sedjo, 2007). For example, in lodgepole pine (*Pinus contorta*) forests regenerating from fire in the Yellowstone region, woody production, live biomass, N mineralization, and total ecosystem C are projected to increase under two different future climate scenarios, with percent increase depending on the climate scenario (Smithwick *et al.*, 2009). Thus, models demonstrate likely changes in forest productivity under future climates; however, without giving specific attention to changes in physiology and C allocation with forest age, they say little about the responses of regenerating forests specifically.

Because disturbance type, severity, size, and frequency affect postdisturbance C dynamics and biogeochemical cycling (Amiro *et al.*, 2010; Smithwick, 2011), future trajectories of forest recovery are likely to be driven by climate change–disturbance type interactions. In most models, disturbance events are generally implemented by altering forest biomass pools through removals (harvest), combustion (fire), or transfer of live to dead material (insect outbreaks), with the amount transferred scaled to disturbance severity. For fire and insect outbreaks, the timing of transfer of biomass to litter and forest floor components varies because tree death can occur slowly, and snag fall rates are dependent on a variety of factors including forest type (Campbell *et al.*, 2007; Edburg *et al.*, 2011). At this time, we are unaware of any model capable of representing the specific dynamics (e.g., recruitment, altered hydrology, or biogeochemistry) associated with distinct disturbance types, severities, and sizes. Therefore, models currently say little about how changing disturbance severity and size are likely to impact forests; however, they do reveal how altered disturbance frequency is likely to impact forests. For example, in the Yellowstone region, fire burn area and frequency are projected to increase under a range of future climate scenarios, quite possibly to the extent that current forest communities will have insufficient time to recover before the next fire event, making the current suite of conifer species unlikely to persist (Westerling *et al.*, 2011). Thus, models demonstrate that climate change is likely to have significant impacts on forested landscapes through its influence on disturbance regimes.

Despite their uncertainties, ESMs have demonstrated that forest recovery will be substantially altered under future climates. Rates of recovery will change, with direction and magnitude varying regionally and depending on future courses of atmospheric CO_2 and climate change. Altered disturbance regimes will inter-

act with altered recovery trajectories, at times driving biome shifts (Westerling *et al.*, 2011). In combination, the direct and indirect effects of climate change are predicted to have substantial impacts on regional C balances and forestry operations; for example, harvestable forest biomass in Canada is projected to be reduced 26–62% for the 21st century, depending on the model assumptions of predicted growth rate, soil carbon decay rate, and area burned by fire (Metsaranta *et al.*, 2011). However, specific representation of physiological and community changes associated with forest age (Table 1) will be required to understand how forest recovery trajectories will be altered by climate change (Fig. 1).

Conclusions

As reviewed above, there is strong evidence that increasing atmospheric CO_2, warming, and altered precipitation regimes will alter trajectories of forest recovery. This conclusion is supported by global patterns in both forest regrowth rates and biomass of mature forests (Fig. 2); responses of forests of various ages to CO_2, temperature, and precipitation manipulation (Fig. 3; Tables S1–S3); observations of altered forest recovery under contemporary multivariate environmental change (Fig. 4); our understanding of successional community dynamics and alternative stable states (Fig. 5); and models. Because forests undergo major structural, physiological, biogeochemical, and compositional changes as they age (Table 1), it is logical that responses to climate change vary as a function of forest age (Fig. 3). Depending on differential responses of forests of different ages, climate change can impact rates of forest recovery, states of mature forests, and/or recovery pathways (Fig. 1, Table 2), and understanding the impact of climate change on forests therefore requires attention to the role of forest age (Fig. 1).

Through its influence on young forests, climate change will impact rates of forest recovery (Fig. 1, Table 2). Multiple lines of evidence point to accelerated regrowth in mesic northern forests under future climates (Figs 2–4; Tables S1–S2); however, responses of tropical forest regeneration rates to elevated CO_2 and increasing temperature remain uncertain. For forests globally, there is strong evidence that biomass accumulation rates will decrease under more arid conditions (Figs 2b and 3; Table S3) – sometimes to the point where forests may never recover (Fig. 5). Changes to rates of nutrient accumulation in biomass, biogeochemical cycling, and community change are likely to parallel responses of biomass accumulation rate (Table 2).

Climate change will also impact the state toward which forests converge as they age (Fig. 1; Table 2). A challenge of central importance is in understanding how climate change responses of young forests – on which the majority of manipulative experiments have been performed (Tables S1–S3) – relate to the ultimate state of these ecosystems once they reach 'maturity' (Fig. 1). For instance, we do not know whether increased biomass accumulation in young forests will translate to increased biomass of old forests or whether these forests will simply attain maximum biomass faster. The effect of elevated CO_2 on mature forest biomass and total ecosystem C remains uncertain, although decreases in either are unlikely; meanwhile, elevated CO_2 is very likely to result in increased nutrient limitation (Fig. 3; Table S1). Likewise, it remains unclear how warming will affect mature forest biomass and ecosystem C stocks (Fig. 3); it is likely that aboveground C stocks will increase in northern climates (Fig. 2c) while soil C stocks decrease and N mineralization increases (Table S2). In contrast, changes in water availability have predictable effects; reduced water availability will reduce productivity, live biomass, and total ecosystem C stocks (Figs 2d and 3; Table S3). In all cases, altered community composition is very likely (Table S3). Responses of mature forest states to combined changes in CO_2, temperature, and precipitation will vary regionally, and understanding how the states toward which future forests will converge as they recovery from disturbance (Fig. 1) remains an important challenge.

Climate change is also likely to impact pathways of forest recovery (Fig. 1; Table 2), which may occur through a variety of mechanisms including altered biogeochemistry (e.g., decreased N limitation during early stages due to increased N mineralization), changing biophysical constraints (e.g., reduced frequency of years with enough precipitation to support seedling establishment), or altered community dynamics. As reviewed above, different species within the same community commonly have substantially different responses to altered CO_2 or climate (Körner *et al.*, 2005; Mohan *et al.*, 2006, 2007; Seiler *et al.*, 2009; Dawes *et al.*, 2011), and consequent changes to community structure may impact ecosystem functioning in ways that cannot be predicted based solely on characteristic physiological responses of dominant taxa (Bolker *et al.*, 1995). For example, increased liana biomass under future climates could meaningfully reduce forest biomass (Phillips *et al.*, 2002; Mohan *et al.*, 2006; Ingwell *et al.*, 2010). Differential responses are likely to be most influential early in succession, when species turnover rate is highest and trees are most sensitive to environmental variation (Table 1), and may have an enduring influence on community composition and ecosystem function (D'Antonio & Vitousek, 1992; Bunker *et al.*, 2005; Beck *et al.*, 2011; Hooper *et al.*, 2012).

Table 2 Probable climate change impacts on trajectories of several forest properties following disturbance (*sensu* Fig. 1)

Forest property	Recovery trajectory	Expected response to climate change			
		Elevated CO_2	Elevated temperature*	Altered water availability	Multivariate change
Biomass	Rate of change	Very likely increase.	Very likely increase in temperate and boreal forests; Uncertain response in tropics.	Very likely increase with water availability/decrease with drought stress.	Likely increase in temperate and boreal forests (absent moisture stress); Likely decrease under drought stress; Uncertain response in tropics.
	Mature state	Uncertain (likely increase or no change)	Possible changes in some regions (e.g., increase in cold regions)	Very likely increase with water availability/decrease with drought stress.	Likely changes (region and time frame specific).
	Pathway	Likely changes driven by shifts in community dynamics, biogeochemistry, or biophysics.	Likely changes driven by shifts in community dynamics, biogeochemistry, or biophysics.	Likely changes driven by shifts in community dynamics, biogeochemistry, or biophysics; High potential for catastrophic shift to low-biomass (nonforest) state under severe drought conditions.	Likely changes driven by shifts in community dynamics, biogeochemistry, or biophysics.
Total C stock	Rate of change	Very likely increases.	Likely increase in temperate and boreal forests; Uncertain response in tropics.	Very likely increase with water availability/decrease with drought stress.	Likely increase in temperate and boreal forests (absent moisture stress); Likely decrease under drought stress; Uncertain response in tropics.
	Mature state	Uncertain (likely increase or no change).	Very likely decrease in soil organic matter, possible increase in biomass carbon (higher latitudes). Net balance uncertain and likely region specific.	Very likely increase with water availability/decrease with drought stress.	Likely changes (region and time frame specific).
	Pathway	Likely changes driven by shifts in community dynamics, biogeochemistry, or biophysics.	Likely concurrent reductions in soil organic C and increases in biomass C.	Likely changes driven by shifts in community dynamics, biogeochemistry, or biophysics; High potential for catastrophic shift to low C (nonforest) state under severe drought conditions.	Likely changes driven by shifts in community dynamics, biogeochemistry, or biophysics (region- and time frame specific).
Biogeochemistry	Rate of change	Likely acceleration of nutrient accumulation in vegetation; Likely acceleration of C & N	Likely acceleration of nutrient accumulation in vegetation in northern forests; Likely acceleration of C & N cycling in temperate and boreal forests;	Likely acceleration of nutrient accumulation in vegetation with increased water availability/rate decrease with drought stress.	Likely acceleration of nutrient accumulation in vegetation in mesic northern forests; Likely rate decrease under drought stress; Uncertain response in tropics.

Table 2 (continued)

Forest property	Recovery trajectory	Expected response to climate change			
		Elevated CO$_2$	Elevated temperature*	Altered water availability	Multivariate change
		cycling in temperate and boreal forests.	Uncertain response in the tropics.		
	Mature state	Likely acceleration of C & N cycling in temperate and boreal forests; Likely decrease in soil N pool; Uncertainty changes total nutrient storage in vegetation.	Likely acceleration of C & N cycling in temperate and boreal forests; Likely decrease in soil N pool; Uncertain response in the tropics.	Likely decrease in nutrient limitation under drought stress.	Likely acceleration of C & N cycling in temperate and boreal forests; Likely decrease in soil N pool; Possible increase in total nutrient storage in vegetation.
	Pathway	Likely increase in nutrient limitation.	Likely concurrent reductions in soil N and increases in biomass N.	Likely changes driven by shifts in community dynamics.	Likely increase in nutrient limitation in mesic forests.
Community composition	Rate of change	Likely acceleration of community change.	Likely acceleration of community change; Uncertain response in the tropics.	Uncertain (drought may reduce the rate of community change through retarded plant growth or enhance it by increasing mortality).	Likely acceleration in temperate and boreal forests (absent moisture stress); Uncertain response in tropics.
	Mature State	Very likely alteration of mature community composition driven by differential species responses; Likely increase in liana abundance.	Very likely alteration of mature community composition driven by differential species responses.	Very likely alteration of mature community composition driven by differential species responses.	Very likely alteration of mature community composition driven by differential species responses; Likely increase in non-native species.
	Pathway	Very likely alteration driven by differential size- and species responses, sometimes causing shift to alternative state.	Very likely alteration driven by differential size- and species responses, sometimes causing shift to alternative state.	Very likely alteration driven by differential size- and species responses, sometimes causing shift to alternative state.	Very likely alteration driven by differential size- and species responses, sometimes causing shift to alternative state.

*Elevated temperature responses assume no change in moisture stress; responses to changes in water availability are listed in 'Altered water availability' column.
'Rate of change' refers to the rate at which the forest approaches its mature state. 'Mature state' refers to the state to which forests converge as they age. 'Pathway' refers to the sequence of states through which any given ecosystem property passes and the relative amount of time spent in each.

In the most dramatic cases, altered successional pathways may result in catastrophic shifts to an alternate stable state (e.g., a forest to grassland transition; Fig. 5). There are documented instances where, following disturbance, young forests fail to establish or persist under conditions that are amenable to persistence of mature forests (Thompson & Spies, 2010; Roccaforte *et al.*, 2012). When these conditions are linked to climate, as they often are (e.g., sufficient moisture for seedling establishment, fire regime), climate change is likely to force a transition to an alternate stable state (Fig. 5). As a result, directional changes to forest ecosystems that would happen gradually in the absence of disturbance may be greatly accelerated by disturbance (Fig. 5).

There remain several important unanswered questions regarding the impact of climate change on the dynamics of forest recovery:

(1) *How does forest age modulate responses to climate change?* Forests of different ages have responded differently to climate manipulations (Fig. 3; Tables S1–S3); however, at this point climate manipulation experiments provide only circumstantial evidence of age differences in climate change response. Systematic comparison of responses of forests of different ages to experimental CO_2 or climate manipulation and to natural climate variability will be crucial to understanding and modeling climate change impacts on forests of all ages.

(2) *How will successional trajectories differ under future climates?* Beyond understanding how age modulates forest responses to climate change, we face the challenge of understanding how climate change will impact entire trajectories of forest recovery (Fig. 1). It is important to note that, because the climate history under which a stand has developed affects its current state and future trajectory, changes to entire trajectories cannot be understood simply by integrating across responses of forests different ages. Rather, it will be important to understand how altered biogeochemical dynamics and community composition shape successional pathways and the states toward which forests converge as they mature.

(3) *Where and when will state changes occur?* Climate change-driven regime shifts (Fig. 5) will have dramatic consequences, yet they remain difficult to document and predict. There is a need for experimental, observational, and modeling studies to identify the conditions under which such shifts are likely and the mechanisms through which they may occur.

(4) *How will tropical forest regeneration respond to climate change?* Although tropical forests are well represented in global-scale comparisons (Fig. 2), precipitation manipulation experiments (Table S3), and long-term monitoring of mature forests (e.g., Chave *et al.*, 2008), we are aware of only one study manipulating CO_2 or temperature at the whole-tree level in a field setting in the tropics (Cheesman & Winter, 2012). This constrains our ability to predict climate change responses of tropical forests. Understanding how climate change will affect tropical forest regeneration is particularly important given the widespread use of slash-and-burn agriculture in the tropics and the significant role of tropical forest regrowth in the global C cycle (Pan *et al.*, 2011).

An additional challenge lies in improved representation of forest recovery dynamics in ESMs, which are currently simplistic in their treatment of forest recovery dynamics. Although detailed representation of forest recovery dynamics in global models is infeasible, we believe that two advances will be important to improving the treatment of forest regeneration. First, the most important stand age-dependent physiology and allocation strategies (driven by aging of dominant species and changes in species composition) should be identified and incorporated. This will allow improved representation of the dynamics of forest recovery in current and future climates. Importantly, this will help to identify situations where young forests fail to establish despite the persistence of their mature counterparts, suggesting climate change-driven regime shifts (Fig. 5). Second, although modeling individual species in ESMs is infeasible, it will be necessary to represent the consequences of demonstrated variability in species responses to climate change and inevitable resultant shifts in community composition and ecosystem processes. With changing community composition, the net ecosystem response may differ significantly from that which would be predicted based on mean characteristics of the original community (Bolker *et al.*, 1995). In the most dramatic cases, altered competitive interactions may result in a regime shift from forest to a grass- or shrub-dominated state (Fig. 5). Predicting regime shifts in ESMs will be particularly important, as these imply feedbacks to the climate system through altered C storage, albedo, and hydrology.

Changes in the dynamics of forest recovery following disturbance will result in potentially significant climate feedbacks. Altered disturbance–recovery dynamics may impact the C cycle enough to reverse the sign of a regional C cycle feedback (Kurz *et al.*, 2008; Running, 2008; Metsaranta *et al.*, 2011). Moreover, albedo and evapotranspiration are important components of the climate regulation services of ecosystems (Anderson-Teixeira *et al.*, 2012), change systematically over the course of forest recovery (Randerson *et al.*, 2006; Kirschbaum *et al.*, 2011; Jin *et al.*, 2012; O'Halloran *et al.*, 2012), and may shift substantially in response to climate change – partic-

ularly if the new community differs dramatically from the old (Beck *et al.*, 2011). Altered forest recovery dynamics will result in particularly strong feedbacks to climate change when a critical threshold is passed such that forests fail to recover (Fig. 5), resulting in dramatic reductions in C storage and altered biophysical properties. For example, in semiarid regions such as the US southwest, current forest communities may not be supported under future more arid conditions and may not re-establish following disturbance, resulting in a positive C cycle feedback (Breshears *et al.*, 2005; Williams *et al.*, 2010, 2013; Anderson-Teixeira *et al.*, 2011; Roccaforte *et al.*, 2012). Thus, recently disturbed forests may play a key role in shaping terrestrial feedbacks to climate change.

This review has demonstrated that the dynamics of forest recovery are likely to be significantly impacted by rising atmospheric CO_2 and climate change. This will have repercussions for biodiversity, climate, and even economics, as the forestry industry and emerging woody bioenergy industry stand to be affected by altered forest regeneration rates (Kirilenko & Sedjo, 2007; Metsaranta *et al.*, 2011; Hanewinkel *et al.*, 2013). Because the course of forest recovery shapes forest structure and function for decades or centuries, climate change impacts on secondary forests will have a lasting legacy. Although the proportion of recently disturbed forests is relatively small at any given time, disturbance eventually affects all forests, and the proportion of forests that have regenerated under altered climate conditions will steadily grow. In these ways, climate change will broadly impact forested regions through its influence on forest recovery dynamics.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of experimental manipulations of CO_2 in tree-dominated ecosystems through Free-Air Carbon dioxide Enrichment (FACE), Open Top Chamber (OTC), or Whole Tree Chamber (WTC; *in situ* only) methodology.
Table S2. Summary of experimental warming in tree-dominated ecosystems (listed in order of forest age).
Table S3. Summary of experimental manipulations of precipitation (PPT) in tree-dominated ecosystems (listed in order of forest age).